

Research review

A research agenda for seed-trait functional ecology

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
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Summary

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Trait-based approaches have improved our understanding of plant evolution, community assembly and ecosystem functioning. A major challenge for the upcoming decades is to understand the functions and evolution of early life-history traits, across levels of organization and ecological strategies. Although a variety of seed traits are critical for dispersal, persistence, germination timing and seedling establishment, only seed mass has been considered systematically. Here we suggest broadening the range of morphological, physiological and biochemical seed traits to add new understanding on plant niches, population dynamics and community assembly. The diversity of seed traits and functions provides an important challenge that will require international collaboration in three areas of research. First, we present a conceptual framework for a seed ecological spectrum that builds upon current understanding of plant niches. We then lay the foundation for a seed-trait functional network, the establishment of

which will underpin and facilitate trait-based inferences. Finally, we anticipate novel insights and challenges associated with incorporating diverse seed traits into predictive evolutionary ecology, community ecology and applied ecology. If the community invests in standardized seed-trait collection and the implementation of rigorous databases, major strides can be made at this exciting frontier of functional ecology.

Introduction

Plant life has diversified enormously since the evolution of seeds (Linkies *et al.*, 2010). Seeds provide evolutionary advantages compared to spores: they enclose and protect embryos, and enable them to survive and develop in places and times too dry for many nonseed plants (Niklas, 2008), store energy and nutrients to support initial development and growth, increasing offspring fitness (Lamont & Groom, 2013), and enable colonization after disturbance and survival during adverse periods (Leishman *et al.*, 2000; Kreft *et al.*, 2010). A range of morphological (e.g. seed and embryo size, coat features) and physiological traits (e.g. light, temperature, water cues) enable seeds to coordinate germination timing with suitable conditions for seedling establishment (Saatkamp *et al.*, 2014; Long *et al.*, 2015). Seed and fruit traits also enable dispersal by animals, humans, wind and water (Poschlod *et al.*, 2013). By reaching more places, persisting over greater timescales, and hence being exposed to a greater range of environmental conditions, seeds increase the likelihood of successful establishment, and subsequent diversification and local adaptation (Donohue *et al.*, 2010). The ability to disperse in space and in time has deep consequences for genetic diversity in plants and, hence, adaptive dynamics (Tigano & Friesen, 2016). These characteristics underscore the central role of seeds in understanding plant ecology and evolution, and how global environmental change will ultimately impact plants and ecosystems. It is therefore a major priority in plant science research to consider both adult and regenerative stages in order to understand how plant traits map to seed functions, the plant niche, community structure and ecosystem functioning (Grubb, 1977).

Traits of seeds and fruits have received less attention in plant science than vegetative traits, except for seed size and mass (Moles & Westoby, 2006; Díaz *et al.*, 2016). We now have a detailed understanding of leaf and root functional traits and their links to ecological gradients and ecosystem functioning (Wright *et al.*, 2004; Mommer & Weemstra, 2012; Sack & Scoffoni, 2013). Functional traits have been defined as measurable features (e.g. seed mass), which interact with ecological factors (e.g. wind speed, water potential) through specific functions (dispersal, germination timing, persistence, establishment) in order to explain plant fitness components (growth, reproduction and survival), ideally measured on individual organisms (Violle *et al.*, 2007). Although this conception fits well for some seed traits (e.g. mass, coat thickness), others are best measured on seed populations and enclose measurements of the environment (e.g. dispersal potential, germination cues, dormancy breaking requirements) approaching seed functions. Understanding how the numerous morphological, physiological and biochemical seed traits map to seed functions is necessary to integrate regeneration traits into ecological strategies

and advance predictive models (Liu *et al.*, 2017). The diversity of seed-related functions makes this a complex but important challenge.

In the present contribution, we envisage a comprehensive research agenda to characterize seed-trait variation and map seed traits to functions, processes and ecological strategies (Fig. 1). A prerequisite to the research priorities outlined below is the development of new databases, or updating and aggregating existing databases, to facilitate the compilation of diverse, standardized and useful (i.e. functional) seed traits at the global scale (Fig. 1, Step 1). A global seed-trait database will pave the way to several emerging and necessary research areas that we develop below (Fig. 1, Steps 2–6). First, we lay the conceptual foundation for a *seed ecological spectrum*, encouraging exploration of trade-offs and ecological strategies during regeneration (see ‘The seed ecological spectrum’ section). We then identify relevant seed traits to be explored for their influence on multiple regeneration functions at a mechanistic level, forming the foundation for trait-based hypotheses. Critical here is the desirability of standardizing and accurately describing seed-trait measurement methodology (see the ‘Mapping seed traits to their functions’ section). Finally, we visit three critical areas of functional ecology to discuss the potential benefits and challenges of exploring: the origin and implications of intraspecific trait variation (see the ‘Intraspecific variation of seed traits’ section); the relationships between seed functions, patterns and processes at the community and landscape levels (see the ‘Linking seed functions to community and landscape dynamics’ section); and the integration of seed traits into applied natural resource management (see the ‘Seed traits in biodiversity conservation’ section).

The seed ecological spectrum

A coordinated effort by many plant ecologists studying how plants optimize productivity, light capture and water use, enabled an understanding of the leaf economic spectrum (Wright *et al.*, 2004; Sack & Scoffoni, 2013). Along with plant height and seed mass, these traits are used to describe the global spectrum of plant form and function (Díaz *et al.*, 2016; Moles, 2018). Likewise, studies of variation in water and nutrient uptake by plants, soil anchorage and the effects of plants on soil moisture, erosion and nitrogen fixation provide a better understanding of the functions of root traits (Mommer & Weemstra, 2012). With the exception of seed size, few seed traits have been included in trait-based ecological studies that aim to understand ecological strategies and predict functions.

Functions linked to fruit, seed and seedling traits have been studied extensively; however, studies that have investigated seed traits often focus on a particular function such as dispersal (Römermann *et al.*, 2005) or persistence in the soil seed bank

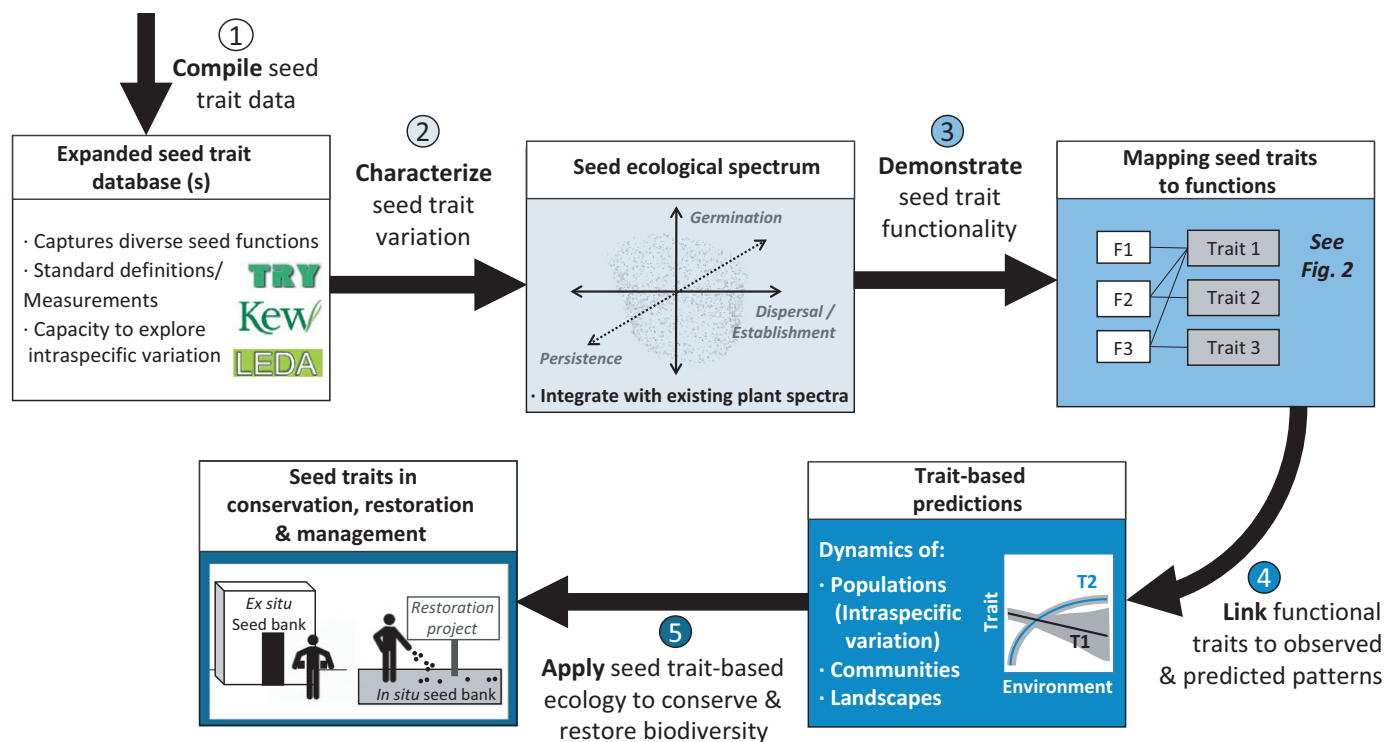


Fig. 1 Five major steps (arrows) leading to five major outcomes (boxes) improving the integration of seed traits into plant science, modelling and management of plant dynamics. Once seed-trait data are accessible in a global databases (e.g. TRY, Kew seed database and LEDA) using standardized definitions and measurements (Step 1), we can explore the key trade-offs that define the regeneration niche, and ask how these patterns add to existing plant spectra (Step 2; see The seed ecological spectrum section). Importantly, seed-trait variation need to be characterized both intra- and interspecifically. We also need to establish links between traits and functions empirically over different environments and scales (Step 3; see the Mapping seed traits to their functions section). These steps will allow us to more effectively integrate intra- and interspecific seed-trait variation into models that improve our understanding of population, community and landscape dynamics by incorporating under-studied regenerative functions and corresponding traits (T1, T2) into updated predictions (see the Intraspecific variation of seed traits and Linking seed functions to community and landscape dynamics sections). Once trait-based predictions are tested and refined, we can use these to inform conservation and restoration practices that rely on plant regeneration from seed (e.g. via *ex situ* conservation seedbanks or *in situ* soil seedbanks) (Step 5; see the Seed traits in biodiversity conservation section).

(Saatkamp *et al.*, 2011), even though their integration may be key for species replacement and community dynamics (Jiménez-Alfaro *et al.*, 2016; Larson & Funk, 2016). We need coordinated studies combining a larger spectrum of seed traits and species to discover how ecological strategies are constructed across regenerative life stages and ultimately influence plant performance in contrasting ecological situations. The lack of a trait-based theoretical framework to understand strategies of plant regeneration from seeds (Funk *et al.*, 2017) is striking given the significance of regeneration traits for adaptation to the environment (Finch-Savage & Leubner-Metzger, 2006; Liu *et al.*, 2017) and the vast amount of information available on seed germination and dormancy (Baskin & Baskin, 2014).

The development of a theoretical plant regeneration framework will require delving into trait trade-offs, which underpin our understanding of multidimensional plant ecological strategies. Although the seed size–number trade-off is well understood as a major dimension of trait variation (Moles & Westoby, 2006), other functional relationships between different axes of seed-trait variation need to be explored, and suggested trade-offs between vegetative and seed traits, such as between seed dormancy and adult longevity (Rees, 1993), need further empirical exploration. Grubb (1977) proposed that the regeneration niche is related to

separate ecological factors (relative to the adult niche) that drive dispersal, seed persistence, germination timing and establishment of new individuals based on outstanding differences of traits during the regeneration phase (Fig. 2). However, little progress has been made in this direction over the last 40 years, and similar questions continue to arise: Are comparable trade-offs detectable among seed traits and functions? If so, are these seed-trait spectra independent of, or coordinated with, resource-related vegetative trait axes?

Although resource allocation in seeds – and hence the ‘economy’ of seeds – is important for different stages of regeneration, it needs to be considered in the larger context of recruitment processes (Pierce *et al.*, 2014). The economic spectra of leaves and roots have their conceptual basis in the allocation of resources to alternative functions that cannot be optimized simultaneously (Wright *et al.*, 2004), but seeds may encompass functions independent of resource economic constraints (Liu *et al.*, 2017). For example, seeds with similar masses may have large variation in germination physiology and their response to environmental factors (Arène *et al.*, 2017) and germination timing might constitute an independent axis of variation compared to morphology and chemistry (Fig. 2). The ability of seeds to disperse, persist, germinate and establish depends on sets of trait-based ecological responses, which, if coordinated

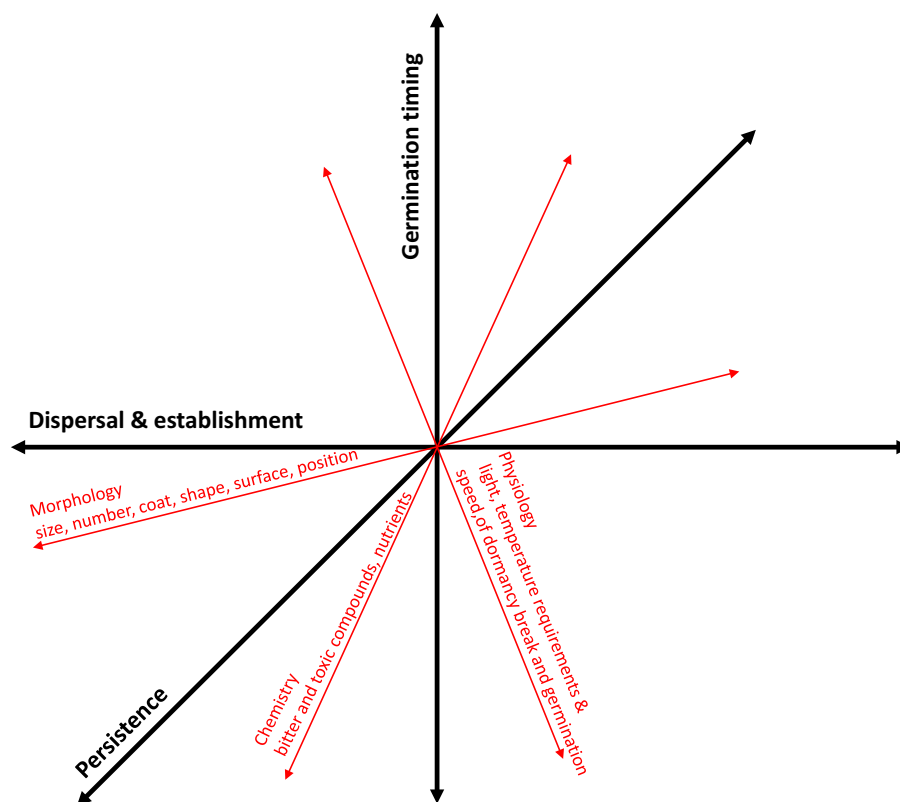


Fig 2 The seed ecological spectrum. We hypothesize that seed traits (red arrows) exhibit trade-offs and axes of covariation linked to several major functions (black arrows). Together, these spectra help to characterize key dimensions of the regeneration niche. A range of seed traits may feed into these spectra (Fig. 3), and whereas the seed size–number trade-off is a well-identified trait set underpinning dispersal and establishment functions, the axes of trait covariation that generate dormancy and germination phenology as well as persistence are still to be quantified. Note that direction and traits on axes are hypothetical.

across individual species, define a *seed ecological spectrum* (SES). We need to understand the functional significance of trade-offs not only between seed size and number (Moles & Westoby, 2006), but also between, for example, physical and chemical defences, or different storage reserves (Davis *et al.*, 2008; Lamont & Groom, 2013). The diverse set of traits regulating seed ecology needs careful and coordinated study in order to identify the main axes of seed-trait variation. A nonexhaustive list of seed traits that might be measured in the SES are listed in Fig. 3.

Understanding the SES also must integrate plant evolutionary history. Notwithstanding early recognition of its importance (e.g. Martin, 1946; Grushvitzky, 1967), the phylogenetic signal of seed traits such as desiccation tolerance (Wyse & Dickie, 2017), dormancy (Willis *et al.*, 2014), embryoless seeds (Dayrell *et al.*, 2017), photo-inhibition (Carta *et al.*, 2017), embryo size (Forbis *et al.*, 2002; Vandeloos *et al.*, 2012) and germination temperature or moisture (Arène *et al.*, 2017) has only been recently quantified in such a way as to be accessible for statistical purposes. Indeed, many other seed traits may show correlations with phylogeny, and many more trait–trait relationships are likely to exist as well, for example between germination speed and seed persistence (Saatkamp *et al.*, 2011; Kadereit *et al.*, 2017). Integrating seed traits that can be collated from experimental studies and analysed at global scales is a research priority, and is necessary to shed light on unknown trade-offs across habitats and biomes.

A collaborative effort by plant ecologists and seed scientists can provide the data and knowledge needed for a global synthesis of the SES. Specifically, we need to: (1) identify the major principles and hypotheses regarding the coordinated ecological responses of seeds to their environment; (2) lay the foundation for global seed-trait databases; (3) establish standardized nomenclature and protocols for filling knowledge gaps on seed traits, complete databases, reducing phylogenetic and geographical biases; and (4) test identified hypotheses with empirical data compiled from global information synthesized in a ready-to-use database. To facilitate synthesis of seed-trait data, we encourage researchers and seed bank managers to share raw germination data together with carefully prepared metadata in a standardized public database. The recent ENSCONET (<http://ensconet.maich.gr>) initiative is a good starting point, but databases should cover a large array of seed traits to really meet the needs for a global understanding on seed functionality.

Mapping seed traits to their functions

In order to guide data collection and empirical efforts endeavouring to integrate seed traits into functional ecology, we propose that focal traits should be targeted in relation to four key seed functions: dispersal, persistence, germination timing and seedling establishment (Fig. 3). These functions capture the essential roles of seeds in

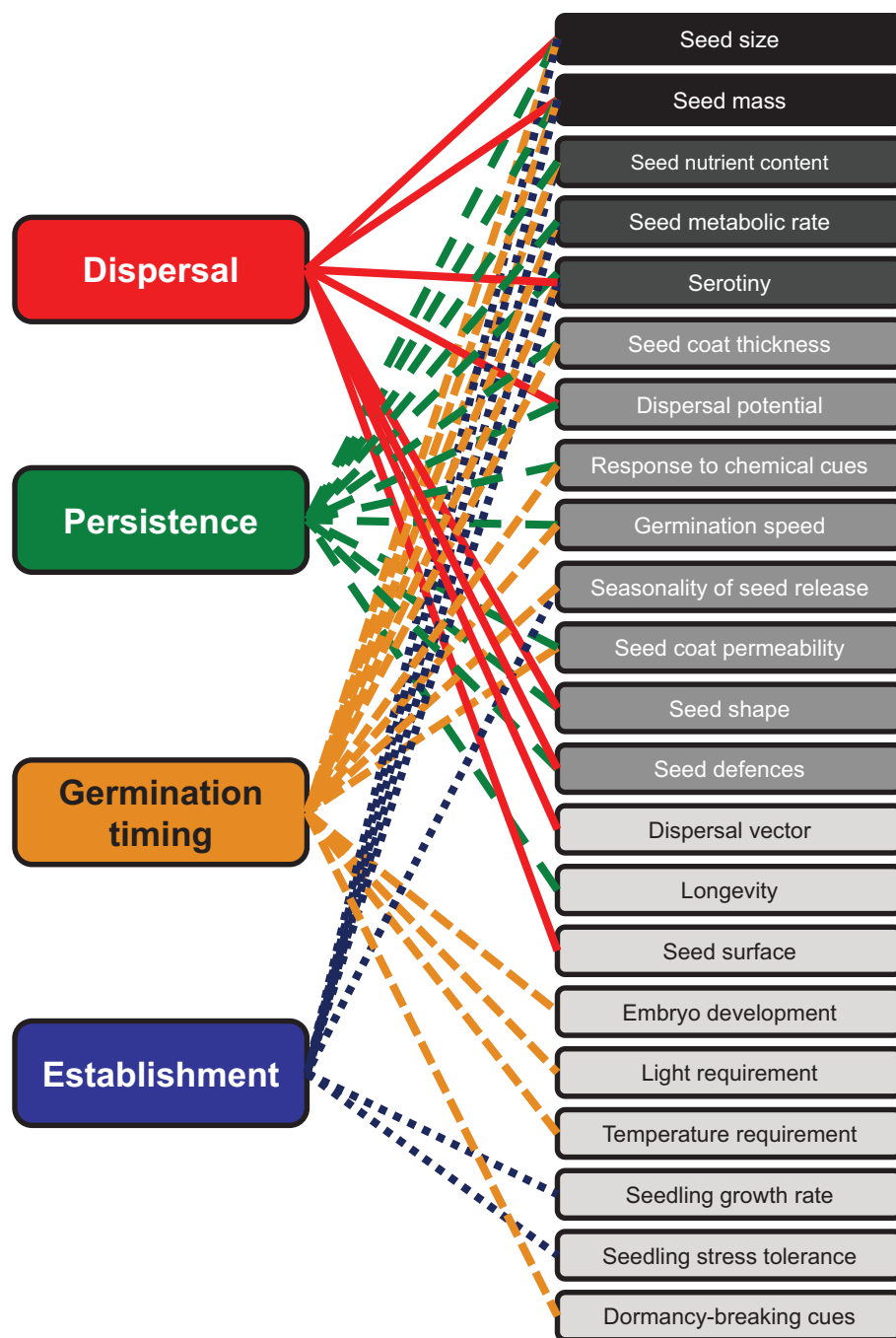


Fig. 3 Network between seed functions (left) and seed traits (right). Lines indicate direct links between traits and functions (coloured). The shading of trait boxes refers to the number of links with seed functions. Dispersal (red) is defined as the horizontal movement of diaspores away from the parent plant. Persistence (green) is the ability of seeds to remain alive in the canopy or soil seed bank and reduce granivory and fungal attack. Germination timing (orange) is the time after dispersal when germination – that is, radicle emergence – occurs; it bridges unfavourable conditions and matches seedling emergence to the optimal moments for regeneration. Seeds can schedule their emergence by dormancy traits and breaking requirements that interact with the seed environment and, once nondormant, with germination traits, such as light and temperature requirements. Establishment (blue) comprises all subsequent functions after germination (emergence, establishment) that result in the successful recruitment of individuals into a population, and also includes seedling traits. Seed traits shown here represent traits broadly (e.g. ‘seed metabolic rate’ is the CO_2/O_2 gas exchange of seeds under standardized conditions; ‘dispersal potential’ is an index based on the percentage of seeds dispersed beyond a reference distance by a specific vector; ‘embryo development’ includes embryo : seed size ratio and embryo growth parameters; ‘seed nutrient content’ represents carbon (C), nitrogen (N), and phosphorus (P) content; ‘response to chemical cues’ include germination response to nitrate, karrikins, etc.; ‘seed surface’ includes seed appendages, hairs, mucilage, etc.; ‘seed defences’ includes content of repellent or toxic substances in the seed coat, e.g. phenols, and mechanical resistance). We plan to publish a handbook that complements this work with detailed definitions, methods of measurements, and standardized data reporting for seed functional traits.

populations, communities and landscapes, and point to research directions for identifying relevant traits and their trade-offs within and across regenerative processes. We suggest a core collection of seed traits, which we expect to be strongly linked to these functions (Fig. 3). Only a few seed traits have been successfully included in mechanistic frameworks, and most still need empirical tests of their hypothesized functions. We therefore suggest the four key seed functions as major 'nodes' of a hypothesized seed-trait network, each of which is connected to multiple traits (Fig. 3) and is implicated in hypothesized dimensions of a seed ecological spectrum (Fig. 2). To understand the origins (see the 'Intraspecific variation of seed traits' section) and implications (see the 'Linking seed functions to community and landscape dynamics' and 'Seed traits in biodiversity conservation' sections) of seed-trait variation, we suggest testing the hypothesized relationships (Fig. 3) and identifying the axes (Fig. 2) in different environmental contexts, at multiple scales, and within and among species and higher taxonomic groups. Most evidently, seed traits also should be analysed together with other plant traits to fully understand their interactions, such as the relationships between plant height and dispersal (Tackenberg *et al.*, 2003), or between life-cycle strategies and seedling establishment.

Dispersal – How do plant traits and their dispersal units operate through biotic and abiotic dispersal vectors to allow seeds to reach favourable sites?

Traits related to this node allow us to better understand how, and how efficiently, seeds disperse to sites optimal for survival, germination and seedling establishment. This includes dispersal to favourable microhabitats for regeneration within an environment favourable for adults, or across unfavourable matrices to spatially restricted habitats. These traits help us to understand how seeds explore new sites, or how populations can persist under locally shifting conditions, and ultimately how seed traits influence shifting distribution ranges with changing environments. Putative traits include not only seed production, but also aspects of seed morphology influencing abiotic travel distance (e.g. seed mass, shape, and surface features such as texture, hairs and appendages) and biotic travel distance (e.g. seed coat thickness, rewards, scent, colour and surface features), traits indicating affinity to a specific dispersal vector, and potential responses to seasonal or global change (e.g. duration and seasonality of seed release).

Seed persistence & germination timing – How do seed traits interact with daily, seasonal and inter-annual variability in environmental factors to avoid or survive temporally unfavourable conditions, and to sense periods of favourable conditions?

Because seeds are the primary recruitment unit of plant populations, it is critical to understand how populations recover via persistent seed banks or freshly dispersed seeds. In many habitats, seedlings are more strongly exposed to hazards *following* germination, so we expect populations to avoid or distribute risk via persistence traits, which enable seed survival until conditions are

favourable for germination and seedling establishment. This holds only for desiccation tolerant (orthodox) seeds, whereas seedling banks play similar roles for species with desiccation sensitive (recalcitrant) seeds (e.g. in moist tropical forests). Germination and dormancy traits also play a critical role in influencing the timing of seed germination in response to environmental factors. Relevant seed traits for persistence increase seed survival between maturation and germination and are related to seed defence, metabolism and resources, which are, in turn, moderated by environmental factors (Fig. 3). For germination timing, seed traits will be related to sensing the optimal regeneration environment through seed coat permeability, germination requirements, chemical cues and dormancy breaking requirements. These germination and dormancy traits lead to a germination timing that not only bridges unfavourable conditions, but also optimizes the fitness of seedlings by delivering germinated seeds at the best moment (Fig. 3). Germination timing covers all aspects ranging from pluriannual regeneration windows such as post-fire or -disturbance, over regeneration seasons (then rather termed germination phenology), to short running constraints such as drying soil after rainfall or growing competitors.

Establishment – How do traits of the germinating seed and seedling interact with local habitat conditions, predators, pathogens and competitors during seedling establishment?

Germination leads into a period of extreme vulnerability, when the transition to autotrophy requires seedlings to overcome multiple potential stressors. This period is influenced by seed-trait properties such as timing of germination, seed carbon, phosphorus and nitrogen content, ratios of lipids, carbohydrates and proteins, as well as traits of the developing seedling such as growth rates, mechanical resistance and seedling stress tolerance, themselves linked to seed traits. We suggest that empirical efforts explore both, with particular emphasis on traits related to biotic interactions of seeds and seedlings with plants and other trophic groups (e.g. fungi, granivores). For example, there is growing evidence that the seed microbiome (Nelson, 2018) has extensive implications for seedling establishment. Finally, in addition to the potential functional importance of establishment traits, we think that in-depth studies of this transitory period present an unique opportunity to better understand links between the ecological strategies of seeds and adult plants. These efforts will pave the way towards incorporating seed traits into the larger picture of plant function (see the 'The seed ecological spectrum' section).

Intraspecific variation of seed traits

Species-level generalizations in functional ecology are at odds with evidence that the explanatory power of trait-based mechanistic models depends on how realistically intraspecific trait variation is represented (Albert *et al.*, 2010; Albert, 2015). Intraspecific trait variability (ITV) is notoriously high for many seed traits, including seed colour, seed appendages, germination requirements and dispersal-related traits (Cheptou *et al.*, 2008; Fernández-Pascual *et al.*, 2013; Guerra *et al.*, 2017), and has important consequences

for seed-related functions (Albert *et al.*, 2011; Cochrane *et al.*, 2015). We therefore need to consider adaptive advantages and sources of intraspecific variation in seed traits.

Intraspecific trait differences can be inherited characteristics of populations (Cheptou *et al.*, 2008; Cochrane *et al.*, 2015) or characteristics that vary as a function of the environment (phenotypic plasticity; Nicotra *et al.*, 2010; Cochrane *et al.*, 2014). In both cases, intraspecific variation could have important implications for regeneration. For example, plants can maximize their long-term fitness by increasing the variability of offspring seed traits, known as bet-hedging in the context of dormancy and germination traits (Tielbörger *et al.*, 2011; Huang *et al.*, 2016). Unfortunately, few studies have considered reaction norms in seed traits and their responses to selection gradients (Cheptou *et al.*, 2008; Nicotra *et al.*, 2015). We therefore need studies investigating the impact of intraspecific seed-trait variability on functions beyond the known cases of variability in dispersal potential (Guja *et al.*, 2014; Albert, 2015), or dormancy-breaking and germination requirements (Huang *et al.*, 2016), especially in situations where dispersers or establishment seasons vary. For example, defence and seedling traits also might exhibit variation that relates to the spatiotemporal variability of predators, pathogens and light conditions.

Seed traits pose an added layer of complexity as they reflect both parental- and offspring-driven effects. Because parent and progeny experience conflicting selective pressures on seed traits, studies need to identify plasticity at different stages. For example, dormancy can vary as a function of developmental conditions via maternal tissue in the seed coat, or as a function of responses to those conditions at the level of endosperm (both parents) or embryo (offspring tissue). Within a species, selection could potentially act on these levels differentially leading to intraspecific variation in dormancy strategies (Valleriani & Tielbörger, 2006; Donohue, 2009).

Underlying mechanisms for intraspecific variation in seed traits include local adaptation, drift, hormonal controls, resource provisioning and epigenetic controls. Unfortunately, we rarely have data on the covariation of the environment of mother plants and seed traits such as germination speed or temperatures (Chen & Penfield, 2018). However, if we are to standardize methods and empirical data on seed traits, we will need to consider how to adequately describe ITV as well as covariates, including relevant variables of the maternal environment. We propose that seed-trait sampling should be sensitive to ecologically important ITV and that researchers should report whether a trait value reflects a mean for an individual, a subset of individuals within a population or a broader collection. Ideally, individual traits might be sampled across populations that represent variation in potential ecological drivers such as rainfall or soil conditions.

Linking seed functions to community and landscape dynamics

Functional traits are increasingly used to understand how abiotic and biotic filters drive community assembly (Götzenberger *et al.*, 2012; Funk *et al.*, 2017). Early studies highlight the role of seed banks and germination as relevant filters (Keddy, 1992; Weiher &

Keddy, 2001) and dispersal, germination timing and seedling establishment have long been seen as key functions to understanding coexistence (Connell & Slatyer, 1977; Grubb, 1977). Surprisingly, however, current models make little use of seed traits in plant community assembly.

When seed-trait variation is incorporated, studies on different phases of community assembly reveal a major role, for example, for dispersal limitation (Schupp *et al.*, 2010; Poschlod *et al.*, 2013) and for persistence (Saatkamp *et al.*, 2014; Gardarin *et al.*, 2015). Variation in seed traits also is pivotal for the tolerance–fecundity trade-off (Muller-Landau, 2010) and for bet-hedging (Venable & Brown, 1988; Tielbörger *et al.*, 2011). Moreover, seed traits enable vegetation to rapidly respond to changes in humidity, light and herbivory (Briggs *et al.*, 2009; Metzner *et al.*, 2017). Finally, seed traits influence soil seed-bank dynamics across seasons and periodic disturbances such as fire (Merritt *et al.*, 2007; Miller & Dixon, 2014). A more complete understanding of community dynamics should therefore include local, seed-dependent functions.

First, we need to deepen our understanding of the interaction between seed persistence in soil and dispersal within communities. The hypothetical trade-off between dispersal and local persistence (Venable & Brown, 1988; Ehrlén & van Groenendael, 1998) does not always show up in data from natural communities (Waal *et al.*, 2015; Metzner *et al.*, 2017), yet it has important consequences for whether community composition changes via migration or seed bank dynamics. Second, although we have a detailed understanding of dormancy breaking and germination cueing (Batlla & Benech-Arnold, 2010; Baskin & Baskin, 2014), we struggle to predict germination dynamics in communities (Larson & Funk, 2016). Predicting seedling emergence could require a detailed understanding of vertical seed movement in the soil, wet–dry cycles and belowground interactions (Gardarin *et al.*, 2012; Saatkamp *et al.*, 2014). It thus remains a major challenge to build mechanistic models of regeneration niches for multiple species.

Limited utilization of seed traits also limits our current understanding of mechanisms that enable coexistence in plant communities, such as seed persistence and adaptive trade-offs in the storage effect (Chesson & Warner, 1981; Angert *et al.*, 2009), shifts in coexistence equilibria resulting from climate change (Kimball *et al.*, 2010) and dispersal–survival trade-offs for diversity in plant communities (Janzen, 1970; McGill & Nekola, 2010). Most trait-based models have missed the role of interspecific variation in regenerative traits for coexistence (Götzenberger *et al.*, 2012; Marques *et al.*, 2014) and, importantly, beyond including those traits that characterize optimal conditions (i.e. the ideal regeneration niche), we urgently need to quantify the range of possible regeneration conditions for each species (regeneration niche breadth).

At the landscape scale, understanding dispersal will be critical to predicting vegetation responses to environmental changes and human impacts. Vegetation patterns that are linked to landscape structure strongly rely on dispersal capacity (Jackel & Poschlod, 2000; Cheptou *et al.*, 2008), and to local seed persistence through temporally varying conditions (Gremer & Venable, 2014; Metzner *et al.*, 2017). The many factors involved in dispersal and subsequent establishment of plants make it difficult to determine which of these

two functions is most limiting at the landscape scale (Poschlod & Biewer, 2005; Guja *et al.*, 2010). Dispersal is linked to seed traits such as seed production and mast fruiting (Bruun & Poschlod, 2006; Visser *et al.*, 2011), rewards for dispersers (Forget *et al.*, 2005; Traveset *et al.*, 2014), terminal velocity (Tackenberg *et al.*, 2003), adhesive seed surfaces (Römermann *et al.*, 2005), seed number per plant, location, season and the duration of mature seed retention on mother plants (Poschlod *et al.*, 2013). Furthermore, in most seed dispersal networks, we are far from knowing how to mechanistically link seed traits to predict effective dispersal distances or vectors (Bullock *et al.*, 2017). Because dispersal effectiveness depends on spatial scale, an important future direction of trait-based ecology will be to incorporate dispersal and establishment limitations, from community to biogeographical scales.

When dispersal moves seeds beyond the climatic or habitat conditions of their mother-plants, additional seed and fruit traits come into play to determine distribution across landscapes: Will seeds survive travelling times during long-distance dispersal? Will there be enough dispersed seeds to establish a viable population? Does the germination niche fit the new conditions? Seed traits could be used to delineate species boundaries by determining the germination niche (Rosbakh & Poschlod, 2014; Arène *et al.*, 2017). Still, we need to better identify which seed and fruit traits are likely to drive species' geographical distributions, and how they can be linked together with vegetative traits in a mechanistic understanding of geographical range shifts (González-Varo *et al.*, 2017).

Seed traits in biodiversity conservation

Research on seed traits provides important knowledge for biodiversity conservation and can inform decisions for *in situ* management of species, populations or communities, *ex situ* seed conservation and ecological restoration. At the population level, seed-based functions such as dispersal and persistence are known to be correlated with population resilience and decline (Römermann *et al.*, 2008), or with habitat fragmentation (Galetti *et al.*, 2013) and management actions impacting ecological processes (Kahmen *et al.*, 2002). Seed traits affecting dispersal (Ozinga *et al.*, 2009) or persistence in the soil seed bank (Stöcklin & Fischer, 1999) can differentially impact species' survival and are therefore an important consideration when managing fragmented populations. Seed traits also can be useful for anticipating responses to land-use change. During assembly, for example, seed traits have been shown to interact with grazing and clear cutting (Piqueray *et al.*, 2015), as well as fire frequency or season (Gomez-Gonzalez *et al.*, 2011; Ooi, 2012), to determine outcomes.

Identifying which seed traits are relevant for management decisions could allow such traits to be integrated into conservation strategies – a particular priority for threatened species (Turner *et al.*, 2018). For example, when managing canopy cover or disturbance, decision-makers may draw upon knowledge of seed size (Kahmen *et al.*, 2002; Jensen & Gutekunst, 2003), gap detection by germination responses (Isselstein *et al.*, 2002) and seasonal germination niches (Kahmen & Poschlod, 2008; Drobnik *et al.*, 2011) to predict and weigh potential outcomes. Knowledge of seed traits

such as shedding phenology, dormancy cycling, burial depth and thermal tolerance could aid management strategies for threatened species in fire-prone ecosystems under a warming climate (Ooi, 2012; Cochrane, 2017). Understanding seed germination timing and persistence also is essential for the conservation of fire-ephemerals and annuals that survive for substantial proportions of their life cycle as seeds in the soil (Cross *et al.*, 2017). Finally, other reproductive traits such as mast fruiting and supra-annual reproductive cycles in many tropical plants will help to evaluate their vulnerability to human impacts (Kelly & Sork, 2002).

Seeds also play an important role in conserving biological diversity, where an understanding of trait variation could impact strategies to add seed material when suitable dispersal vectors are unavailable or when plants have reduced soil seed-bank persistence (Poschlod & Biewer, 2005; Kiehl *et al.*, 2010). There also are opportunities to draw on seed-trait variation to manage invasive species based, for example, on the time or chemical cues necessary to deplete seed banks, or germination season and the effect of fire on germination (Long *et al.*, 2015). Germination timing also has been shown to be critical in determining competition outcomes with invasive species (Gioria & Pyšek, 2017). Because trait-based inferences can reduce uncertainty and facilitate generalization to rare species, populations or communities, future syntheses on seed-trait functions will provide an invaluable resource for biodiversity conservation.

The ongoing decline in plant diversity also has demanded *ex situ* management practices, one of the most practicable being the external storage of seeds in gene banks. Seed traits are likely to be intrinsically linked to seed survival in long-term storage, although identifying and quantifying seed traits related to longevity and desiccation tolerance, while also partitioning environmental drivers, can be challenging (Probert *et al.*, 2009; Hay & Probert, 2013). Landmark studies have uncovered functional traits associated with seed longevity in *ex situ* storage (Probert *et al.*, 2009; Merritt *et al.*, 2014), yet there are likely many insights to be gained by demonstrating the functions of those traits. Some traits such as seed mass have been associated either positively (Moles & Westoby, 2006) or negatively (Thompson *et al.*, 1998) with seed longevity in different studies, leaving an additional uncertainty about how to relate field and experimental findings. Therefore, a comprehensive global assessment focused on linking traits to external seed storage responses could yield many new trait-based insights to inform *ex situ* conservation practices. A greater awareness of seed traits, their functions and phylogenetic distribution (Wyse & Dickie, 2017) is relevant not only for effective seed banking practices, but for countries to effectively meet the targets of the Global Strategy for Plant Conservation (COP, 2002).

Seed banking and evaluation of early life-history traits is in many cases a prerequisite for successful ecological restoration (Miller *et al.*, 2017). Large-scale restoration often relies on seed, and therefore on knowledge of seed production, dormancy and germination characteristics (Merritt & Dixon, 2011). These traits may be key for determining the suitability of species for restoration (Perring *et al.*, 2015; Ladouceur *et al.*, 2018), for optimizing pre-treatments to enhance performance such as emergence (Commander *et al.*, 2017; Erickson *et al.*, 2018) and drought tolerance (Lewandowski *et al.*, 2016), for understanding when and where

seeds may germinate (Commander *et al.*, 2017), or for promoting germination by applying specific cues (Tieu, 2001). The interaction between seed traits and abiotic factors such as soil physico-chemical properties may influence seedling emergence patterns and consequently seedling community composition in restored areas (Merino-Martín *et al.*, 2017a). In addition, insight into seed functional traits may provide restoration managers with a better understanding of why seedling recruitment may fail (Merino-Martín *et al.*, 2017b). Although trait-enhanced colonization may be a focus early in restoration efforts, traits linked to seed bank persistence and dispersal are increasingly recognized as important determinants of long-term success (Pywell *et al.*, 2003). Seed bank persistence is of particular importance to restoration projects that use topsoil as a seed source. A better understanding of the seed traits that enable seed persistence in stockpiled topsoil, and ways to manage the seed bank in receptor sites, will lead to improved restoration outcomes (Buisson *et al.*, 2018).

Epilogue

Our knowledge of plasticity, adaptation, evolution, distribution and dynamics of plants needs to include a deeper understanding of seed traits and functions to anticipate how biodiversity will respond to human impacts, and how to preserve natural ecosystems. Once we identify seed traits and functions related to seed dispersal, persistence, germination timing and establishment, the goal for ecologists will be to incorporate these traits into our understanding of ecological and evolutionary processes across organizational and spatiotemporal scales. Our research agenda is based on functional seed traits with strong impacts on plant populations with the potential to predict diversity patterns and processes at different spatiotemporal scales, to assess the vulnerability of species and communities that are most vulnerable to global changes, to support the prioritization of conservation actions and to promote ecological restoration, securing provisioning of food and ecosystem services for a growing human population.

In order to develop a robust seed-trait database and enable larger scale comparisons, we need to synthesize the different methodologies used to measure seed traits. Although some trait measurements may be standardized, it is important to report the methodologies in sufficient detail and with relevant metadata, because it is often meaningful to measure seed traits in different ways. For example, when considering dispersal, fresh dispersule weight might be relevant, whereas dry weight may be a better indicator of available resources when studying seedling survival.

In the present contribution, we call for a global seed-trait database that will facilitate exploration of the seed ecological spectrum, opening a black box in functional ecology and allowing a more integrated view of plant function across all life stages. A global database of seed traits will be of pivotal importance for biological conservation in a world with increasing human impacts on vegetation, which is being devastated, regenerated and/or restored. We also need a comprehensive definition of the seed traits and functions that have been introduced here, using standardized methods to measure traits from existing datasets or from the experiments that seed ecologists will conduct in the following

years. Finally, to improve long-term conservation and restoration successes across multiple generations, we advocate for increased research into each of the four seed functions in applied contexts. Such research will drive a shift from degradation- and ecosystem-specific restoration strategies to a generalized knowledge of traits that guide restoration strategies and increase their success. These challenges will require funding and international coordination among seed scientists and plant ecologists encompassing different views and disciplines.

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Author contributions

ASaatkamp, AC, LC, LKG, BJ-A, JL, AN, PP and FAOS wrote the manuscript; ASaatkamp, AC, LC, LKG, BJ-A, JL, AN, PP, FAOS, ATC, ELD, JD, TEE, AFidelis, AFuchs, PJG, MH, WL, DJM, BPM, RGM, CAO, MKJO, ASatyanti, KDS, RT, STomlinson, STurner and JLW contributed to design, performance of research, writing and revision of the manuscript.

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